



## **Eclipse effects on field crops and marine zooplankton: the 29 March 2006 Total Solar Eclipse**

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# Eclipse effects on field crops and marine zooplankton: the 29 March 2006 Total Solar Eclipse

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## Abstract

The effects in the biosphere from the Total Solar Eclipse of 29 March 2006 were investigated in field crops and marine zooplankton. Taking into account the decisive role of light on the photoenergetic and photoregulatory plant processes, measurements of photosynthesis and stomatal behaviour were conducted on seven important field-grown cereal and leguminous crops. A drop in photosynthetic rates, by more than a factor of 5 in some cases, was observed, and the minimum values of photosynthetic rates ranged between 3.13 and 10.13  $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ . However, since solar irradiance attenuation has not at the same time induced stomatal closure thus not blocking  $\text{CO}_2$  uptake by plants, it is probably other endogenous factors that has been responsible for the observed fall in photosynthetic rates. Field studies addressing the migratory responses of marine zooplankton (micro-zooplankton (ciliates), and meso-zooplankton) due to the rapid changes in underwater light intensity were also performed. The light intensity attenuation was simulated with the use of accurate underwater radiative transfer modeling techniques. Ciliates, responded to the rapid decrease in light intensity during the eclipse adopting night-time behaviour. From the meso-zooplankton assemblage, various vertical migratory behaviours were adopted by different species.

## 1 Introduction

On 29 March 2006, millions of people in the Northern Hemisphere had the opportunity to observe a total solar eclipse. In the Greek territory, the phenomenon had a maximum duration of 2 min and 58 s, at the small island of Kastelorizo in the east-southern part of the country.

The effects of solar eclipses on the behaviour of living organisms have been the subject of many observations. Plant behaviour was first studied by Deen and Bruner (1933) by following stomatal movements of the gray birch during the sun eclipse of 1932. Two Polish zoologists were the first to observe the behaviour of mammals, birds,

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and insects during seven eclipses between 1954 and 1975 (Zirker, 1995). More recent data have shown that birds behave as they normally do at sunset (Tramer, 2000), animals alter their behaviour (Jennings et al., 1998) and some planktonic crustacea are vertically redistributed (Vecchione et al., 1986; Giroud and Balvay, 1999).

In general, eclipse effects on plants are expected to be related to the light limitation experienced during the phenomenon. Although fluctuating light conditions are a common feature for natural habitats (e.g. through transitional light flecks in canopies, changing cloudiness, diurnal periods of light and dusk), the dynamics of the decline of radiation during an eclipse typically differ (Schulze and Hall, 1982; Kupperts et al., 1997). Moreover, observations have shown that a drop of sap flow in a number of plants was related to solar eclipses (Ladefoged, 1963; Fernandez et al., 1996; Morecroft et al., 2000).

Developmental processes, such as transient aberrations in the chromosomal structure of root meristems and a delaying seed germination, have been also ascribed to the impact of an eclipse (Sathalah et al., 1984; Kumar et al., 1984). In addition, limited short-term effects on photosynthesis and evapotranspiration of crop plants, such as pigeon pea and bread wheat, were reported by Singh et al. (1992). In mature forest trees of *Picea abies*, *Fagus sylvatica* and *Quercus robur* photosynthesis was reduced to an extent that allowed net CO<sub>2</sub> evolution from leaves during an eclipse (Häberle et al., 2001).

The effects of solar eclipses on marine ecosystems have been partially studied. Pepita (1955) reported an upward migration of free-swimming larvae of shrimps, clams, snails and barnacles, as well as of adult copepods during the period of maximum totality, in Sebastopol Bay. Skud (1967) observed a decrease in zooplankton volumes at surface waters in Maine, although he reported an upward migration of two copepod species (*Pseudocalanus minutus* and *Acartia longiremis*), during the time of darkness. Adult copepods moved upwards in the water column during an eclipse event observed in the region of Boothbay harbor, Maine, in March 1970 (Sherman and Honey, 1970). Similarly, Bright et al. (1972) found that certain species of copepods and euphausi-

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aceans (e.g. *Nannocalanus minor*, *Scolecithrix danae* and *Undinula vulgaris*) in the Gulf of Mexico, responded to the noontime solar eclipse of March 1970 by migrating to the surface. Moreover, according to Bright et al. (1972), the response as reflected in the number of organisms captured at the surface, was larger than the respective response to a decrease in light intensity at night. Some studies of the movements of scattering layers during solar eclipses showed that layers started ascending at the beginning of the eclipse (Backus et al., 1965; Tont and Wick, 1973; Kampa, 1975), while in other cases the scattering layers did not respond at all (Franceschini et al., 1970).

The diurnal vertical migration of many zooplankters is a well known behavior, with some of the organisms migrating several hundred meters in the water column (Marshall and Orr, 1955; Longhurst, 1976). The factors controlling vertical migration in mesopelagic species, however, have not been intensively studied. It is generally accepted that down-welling irradiance plays an important role (Banse, 1964; Ringelberg, 1995), since most vertical migrations of plancton occur at sunrise and sunset. Although, most of the above studies concern mesozooplankton there is lack of information concerning other zooplankton organisms.

This study aims at investigating the effects of solar eclipses on field crops and marine zooplankton in Greece, during the 29 March 2006 total solar eclipse. Since there is no available evidence on the mechanisms involved in the effects of solar eclipses on photosynthesis and stomatal behaviour, and taking also into account the decisive role of light on the photoenergetic and photoregulatory plant processes, this has been an excellent opportunity. A total solar eclipse, providing a sort of artificial night, offers the possibility to study the migratory responses of marine organisms. Field studies addressing this issue are scarce, primarily because of the difficulties associated with measuring rapid changes in underwater light intensity, simultaneously with changes in animal distributions. In this study, this has been overcome with the use of accurate underwater radiative transfer modeling techniques.

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2 Materials and methods

2.1 Photosynthesis and stomatal conductance in field crops

2.1.1 Study site

The study was carried out in the experimental field of the Agricultural University of Athens (37°59' N, 23°32' E), at an altitude of 30 m a.s.l. The site was located about 560 km from the central axis of the eclipse totality, with 84% sun obscuration. The crops have been growing in a slightly alkaline (pH 7.24) clay loam soil (35.9% sand, 35.9% silt and 29.8% clay) over an area of 400 m<sup>2</sup>.

2.1.2 Plant material

Seven important field-grown cereal and leguminous crops were studied. In particular, the studied crops were: cereals [*Triticum durum* (durum wheat), *Tr. aestivum* (bread wheat), *Hordeum vulgare* (barley), *Avena sativa* (oat)] and legumes [*Lathyrus sativus* (grass pea), *Pisum sativum* (pea) and *Vicia faba* (faba bean)]. During the eclipse case study all cereals were at the booting stage and the legumes at flower appearance. The measurements were taken on the third leaf from the top for the cereals and on the leaves at the middle of the stem for the legumes.

2.1.3 Measurements of photosynthesis and stomatal conductance

The chlorophyll fluorescence technique was used to measure the photosynthetic activity of leaves. Net photosynthesis (Pn) and stomatal conductance (*g<sub>s</sub>*) were measured in the field using a closed portable Infra-Red Gas Analysis (IRGA, LI-COR, LI-6200 model) system. The top leaf was enclosed in a 4 litre chamber connected to the IRGA, and the instrument was moved from crop to crop for consecutive measurements within less than one minute. Air flow rate into the IRGA system was 800 μmole s<sup>-1</sup>. Photosynthetic Active Radiation (PAR) measured with a quantum sensor connected to the

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chamber, was found to be  $1700 \pm 150 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ . Pn and  $g_s$  calculation was based on the equations of Leuning and Sands (1989) and are expressed as  $\mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$  and  $\text{mole m}^{-2} \text{s}^{-1}$ , respectively. Hourly measurements were carried out during 6:00–17:00 UTC on 29 March 2006.

Additional meteorological and actinometric data monitored at Thission station (National Observatory of Athens) were used in this study. Information about the station characteristics and infrastructure used can be found in Founda et al. (2007).

## 2.2 Marine zooplankton

### 2.2.1 Study site and hydrographic measurements

One oceanographic cruise on board the R/V AEGAIO was carried out on 29 March 2006, at a fixed station close to Kastelorizo Island in the Eastern Mediterranean ( $36^\circ 08' \text{N}$ ,  $29^\circ 34' \text{E}$ ). Downward surface global (200–850 nm) and direct (280–700 nm) irradiance spectra were measured during 9:00–13:00 UTC at a sampling frequency of 20 s and 8 s, respectively, using two diode-array spectrometers (Kazadzis et al., 2007; Blumthaler et al., 2006).

The water column structure was sampled before, during, and after the eclipse, at approximately 1 h intervals, during an 8 h period (Table 1). Vertical profiles of temperature and salinity were measured with a Seabird CTD System (911 plus) assembly. Phytoplankton fluorescence (Chl-a) was recorded with a Chelsea in situ fluorometer. Water samples were taken in the euphotic 0–100 m layer, using Niskin bottles with teflon-coated springs and O-rings. For microzooplankton, 7 replicate samples were taken hourly, every 10 m in the water column, whereas for mesozooplankton, 6 replicates of samples were collected hourly at discrete layers (0–10 m, 10–20 m, 20–50 m, 50–100 m, 100–200 m).

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2.2.2 Zooplankton measurements

Five hundred ml micro-zooplankton samples were preserved with borax-buffered formalin (final concentration 2% formaldehyde) and stored at 4°C in the dark. Before examination, samples were left to settle in their bottles in the dark at 4°C and after 48 h, the top 400 ml of the sample was slowly siphoned off. The bottom 100 ml of the sample was transferred into sedimentation chambers, allowed to settle for 24 h (Utermohl, 1951) and was finally examined by means of an inverted microscope OLYMPUS IX 70.

Meso-zooplankton was sampled by vertical hauls of a WP-2 net (200 µm mesh size). Samples were fixed immediately after collection and preserved in a 4% borax buffered-formaldehyde seawater solution. In the laboratory the samples were split using a folsom splitter. The first half was used to get information on the taxonomic level of order or species and counted under an OLYMPUS stereoscope.

2.2.3 Underwater radiative transfer modeling

Measured changes in above water light intensity and underwater composition during the solar eclipse, were used as input to the extensively validated Hydrolight Radiative Transfer Program (Mobley, 1988), to estimate changes in underwater radiation fields. In the absence of in situ underwater radiometric measurements, the model calculations allowed us to estimate the changes in light levels (e.g. PAR) at specific depths in the water column, where changes in micro- and meso-zooplankton concentrations were observed during the solar eclipse event. Mobley (1994) has given a detailed description of the physical assumptions and mathematical calculations in the Hydrolight Model. Tzortziou et al. (2006) recently reported very good agreement (differences less than 10%) between in situ measurements of water leaving radiance and Hydrolight results, over a wide range of conditions in the bio-optically complex estuarine waters of the Chesapeake Bay, and demonstrated very good optical closure between independently measured quantities.

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Measurements of downward surface irradiance spectra,  $E_s(\lambda)$ , and chl-a vertical profiles were used as inputs to perform the model calculations. The water was modeled by three components: pure water, pigmented particles and covarying colored dissolved organic matter (CDOM). We assumed that mineral concentrations were negligible in the very clear, oligotrophic waters at the Kastelorizo site.

The Pope and Fry (1997) absorption values for pure water and the seawater scattering coefficients of Morel (1974) as retabulated by Smith and Baker (1981), were used in our model simulations. Particle absorption at depth  $z$  and wavelength  $\lambda$ ,  $a_p(z, \lambda)$ , was estimated using the Morel (1991) model and the chlorophyll-specific absorption coefficients given in Prieur and Sathyendranath (1981). Absorption by CDOM,  $a_{\text{CDOM}}(z, \lambda)$ , was assumed to covary with particle absorption according to  $a_{\text{CDOM}}(z, \lambda) = 0.2 \cdot a_p(z, 440) \cdot \exp[-0.014 \cdot (\lambda - 440)]$  (Mobley and Sundman, 2000). Particulate scattering was estimated using the Gordon and Morel (1983) model, while CDOM was assumed to be non-scattering. Because measurements of particulate backscattering were not available, a backscattering fraction of 0.044 was used in our calculations based on previous studies for clear waters (e.g. Mobley, 1994; Stramski et al., 2004). Raman scattering and CDOM and chlorophyll-a fluorescence were included in all model runs using the Hydrolight default assumptions for fluorescence efficiency and wavelength redistribution functions for fluorescence by chlorophyll (Mobley, 1994) and CDOM (Hawes, 1992).

Water surface roughness was estimated assuming that the slope probability distribution of the capillary waves follows the Cox and Munk (1954) wind-direction independent distribution. A wind speed of  $5 \text{ m s}^{-1}$  was used in the simulations based on local meteorological observations. The water column was assumed to be infinitely deep below the greatest depth of interest (ca. 250 m). Model results included underwater vertical profiles of photosynthetically active radiation, PAR (in  $\mu\text{mol phot m}^{-2} \text{ s}^{-1}$ ), estimated according to Mobley (1994) from underwater scalar irradiance,  $E_o(z, \lambda)$ , and integrated over the spectral region 400–700 nm.

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### 3 Results and discussion

#### 3.1 The effect of the solar eclipse on photosynthesis and stomatal conductance

On 29 March 2006, the eclipse effects on the biosphere and on various atmospheric layers have been investigated during a combined field experiment over Greece. Information about the experimental campaigns, the measurement sites, eclipse path maps and eclipse local circumstances at each location, can be found in the overview paper by Gerasopoulos et al. (2007).

The diurnal course of meteorological parameters during 29 March 2006 is shown in Fig. 1. Solar global irradiance (Fig. 1a) displayed a sharp decline of  $796 \text{ W m}^{-2}$  during the eclipse, in comparison with the pre-eclipse maximum. A decline was also exhibited in air temperature ( $2.2^\circ\text{C}$ , Fig. 1b) and atmospheric pressure ( $0.7 \text{ hPa}$ , Fig. 1d). On the other hand, relative humidity increased by about 10% (Fig. 1c). The combination of light “switch off” and increased humidity, together with the decreased temperature during eclipses has been previously shown to have an impact on forest trees (e.g. Steppe et al, 2002).

Figure 2 illustrates the diurnal course of photosynthetic rate for the cereals and legumes examined. A drop in photosynthetic rates, by more than a factor of 5 in some cases, was observed as a response to the variation in PAR during the eclipse. The minimum values of observed photosynthetic rates ranged between  $3.13$  (faba beans) and  $10.13 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  (bread wheat). The relative reduction of photosynthesis during the eclipse varied among the different species (Table 2, Fig. 2). Faba beans, oats and grass pea were the most intensely affected, in contrast to whereas bread wheat, pea, barley and durum wheat. In general, cereals were less influenced than legumes; with min/max ratios on average  $0.31$  and  $0.24$ , respectively.

Given that the minimum irradiance during the eclipse was equivalent to that recorded at 16:00 UTC (about  $62 \text{ W m}^{-2}$ ), it is not surprising that the rates of photosynthesis at totality were roughly similar to those observed at 16:00 UTC. Thus, the effects of solar eclipse on photosynthesis resemble those obtained at dusk in agreement with

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Matyssek (1986) and Häberle et al. (2001).

One-way ANOVA was applied, on three replicates for each plant, in order to test the statistical significance of the variance in stomatal conductance ( $g_s$ ). Table 3 shows the diurnal changes of  $g_s$  for the examined species. In all species except pea,  $g_s$  showed a decline at 10:00 UTC and at earlier eclipse stages, occasionally significant (e.g. in bread wheat, oats, and faba beans) in comparison with the preceding values. At 10:30 UTC however a time near the totality,  $g_s$  returned to values before the beginning of the eclipse, maintained throughout the rest of the day. Thus, the drop in  $g_s$  at 10:00 UTC is probably not eclipse induced and an additional important argument is that the timings of minimum  $g_s$  and minimum photosynthetic rate do not coincide.

From the above it is evidenced that the diurnal course of  $g_s$  followed the typical pattern expected for mesophytic crop species: higher values early in the day 6:00–7:00 UTC, steadily declining within the next two-three hours and remaining stable thereafter. It is also known that morning values of  $g_s$  are higher than those observed in the afternoon for similar PAR (Rochette et al., 1991). A midday temporary decrease in  $g_s$  is also a common phenomenon in dry environments, like the one of southern Greece. Accordingly, the drop in  $g_s$  observed at 10:00 UTC simply reflects normal, “midday stomatal closure” (Miller, 1938; Meidner and Mansfield, 1968).

Stomatal movements are greatly affected by environmental conditions. Light is reported to be amongst the most important factors determining the course of stomatal behaviour (Meidner and Memmsfield, 1968), although many interactions with other environmental (e.g. CO<sub>2</sub>–concentration, vapour pressure deficit, temperature, etc.) and plant factors (plant water status, endogenous rhythms) exist to a considerable extent. It is obvious from our results that the solar eclipse has influenced photosynthesis (Fig. 2) but on the other hand it was not an important factor directly affecting the course of  $g_s$  (Table 3). Consequently, since solar irradiance attenuation has not induced stomatal closure thus not blocking CO<sub>2</sub> uptake by plants, it is probably other endogenous factors coupled with the absence of light that has been responsible for the observed fall in photosynthetic rates.

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Photosynthesis is inherently dependent on light. The three functions of the light harvesting apparatus (light capturing, energy transfer and electron transfer) are controlled by the physical and chemical characteristics of the plant pigments. Absence of light disrupts electron transport, leading to a decline of photosynthesis (Schreiber et al., 1995).

- 5 This sequence of events also occurs during a solar eclipse which, to some extent, resembles the daily dawn and dusk periods with their gradual changes in PAR. However, in contrast with normal diurnal courses, the time span of the decline in PAR and its subsequent recovery during a total solar eclipse last for only a few minutes each, which is much shorter than the duration of dawn and dusk in the temperate climates.

## 10 3.2 The effect of eclipse on marine zooplankton

The solar eclipse induced effects on ecosystems has been additionally investigated in the marine environment. These effects are mainly driven by the change of underwater irradiance that has been simulated via the Hydrolight Radiative Transfer Program for the case of Kastelorizo. Figure 3 shows the change with time in downward irradiance as measured above the water surface,  $E_s$ , during the eclipse event. Light intensity dropped dramatically with the onset of the eclipse, with  $E_s$  at 550 nm decreasing from  $\sim 1.35 \text{ W m}^{-2} \text{ nm}^{-1}$  at 9:35 UTC (1st contact) to below the range of the instrument's sensitivity during totality 10:53 UTC, increasing again to  $\sim 1.16 \text{ W m}^{-2} \text{ nm}^{-1}$  at 12:10 UTC (last contact). Model estimated photosynthetically active radiation (PAR)

15 just below the water surface was  $\sim 2000 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$  just before the 1st contact, while the evolution of PAR at more depths (10 and 30 m) is also shown in Fig. 3.

The water column structure at the sampled station before, during and after the eclipse is described in Fig. 4. Temperature and salinity ranged from 16.2 to 17°C and from 39 to 39.2 psu, respectively, in the upper 200 m. Due to spring warming, the surface layer (from the surface down to 20–30 m) is warmer and saltier than the underlying waters, transported in the area by the Asia Minor current (POEM group, 1992). The water mass under the thermocline is the Levantine Intermediate water, with almost homogenous temperature and salinity extended down to 250 m. Temperature and salinity

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remained almost constant during the eclipse event. Chl-a concentration varied from 0.14 to 0.19  $\mu\text{g l}^{-1}$ , with a small chlorophyll maximum between 40 and 60 m. No significant changes in chl-a vertical distribution were observed during the eclipse event.

## Ciliates

5 The ciliate community included members of the orders Choreotrichida (*Strobilidium* spp, *Lohmaniella* spp), Tintinnida, Oligotrichida (*Strombidium* spp, *Tontonia* spp and *Laboea* spp). Cell numbers were dominated by small oligotrichs 20-30  $\mu\text{m}$  (35-75%).

From the vertical abundance profiles (Fig. 5, K1 and K3) it was clear that before the eclipse ciliates showed a non-random distribution and tended to accumulate at 30 m depth, where they showed a distinct peak in cell numbers (up to 212 cells  $\text{l}^{-1}$ ). At this  
10 depth, PAR was  $\sim 11\%$  of its surface value (cast K2 in Fig. 6).

However, at 10:20 UTC (cast K4), one hour after the 1st contact and 30 min before totality, we observed a vertical homogenous spreading of the ciliates in the water column. At this time, surface PAR had already decreased by  $\sim 50\%$ . It seemed like ciliates  
15 responded to the rapid decrease in light intensity during the eclipse, adopting a night-time behavior. At 11:20 UTC (cast K5), almost 30 min after totality, when surface PAR was  $\sim 35\%$  of its initial value before the eclipse, ciliates were found in greater numbers within the first 20 m from the surface. Two hours after totality (cast K6 at 12:50 UTC), the notable peak at 30 m was re-established.

20 Ciliate diel cycles have been surprisingly little studied before. Jonsson (1989) reported that ciliates often accumulate around the pycnocline, mainly due to the effect of negative geotaxis. Chemokinetic and photokinetic responses have been shown to influence the vertical distributions in some ciliates in lake environments (Finlay et al., 1987). Interactions between sinking velocity, swimming velocity, tumbling rate and  
25 shape or density asymmetry of the cell have also been suggested to explain the vertical distribution of planktonic ciliates in natural waters (Jonsson, 1989). Perhaps the ciliate community tried to stay within its optimal photo-environment during the unusually rapid decrease in light intensity due to the eclipse. Vertical migration could also

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be governed by other factors, such as predation. Ciliates could move downwards in order to avoid predation pressure from zooplankton, accumulated near the surface layers at night. Perez and Dolan (1995) found in a study at the Western Mediterranean sea, that chlorophyll containing ciliates were mainly concentrated at the chl-a maximum depth, however heterotrophic ciliates often migrated from 20–30 m depth during the day to the surface at night or in the early morning. Measurements by Stoecker et al. (1989) across Georges Bank (Northwest Atlantic), revealed that oligotrichous ciliates with chloroplasts were usually located in the upper half of the euphotic zone during the day, showing diel changes in their distribution pattern. For example, *Laboea strobila* was concentrated near the surface just before sunrise and early in the morning, but had a subsurface maximum at noon.

## Mesozooplankton

The mesozooplankton assemblage was made up 39–74% by copepods, showing an increasing relative abundance with depth. Copepodites of *Clausocalanus*, *Paracalanus*, *Oithona* and *Ctenocalanus* dominated the copepod assemblage (up to 40, 42, 19 and 15% respectively). Less important were *Clausocalanus paululus*, *Ctenocalanus vanus*, *Oithona plumifera* and *Oncea media* (up to 8–10%). The non-copepod zooplankton made a significant contribution to the total abundance represented, by 5 taxa: Appendicularia, Doliolidae, Chaetognatha, Medusae and Pteropoda.

Figure 7 shows the results of copepod vertical distribution at the surface down to 100 m. Copepods exhibited the greatest density between 10–20 m depth. At K4 10:20 UTC when surface PAR was ~50% (Fig. 6) of that before the eclipse, copepods showed higher abundance close to the surface which can be explained by a possible migrating behaviour. *Calanus* and *Clausocalanus* copepodites seemed to be synchronized with the exogenous changes of light due to the eclipse. Individuals of these species showed a vertical migratory movement towards the surface. Among the other copepodites, *Paracalanus* mainly localized at 0–10 m increased their abundance in this layer before totality. *Oithona plumifera* collected mostly in the 10–20 m

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tows appeared in greater abundance in the 0–10 m layer, as well as *Oncea media* concentration increased at the surface layers. The other copepodites, male and female copepods displayed no significant differences in distribution and apparent response to the eclipse.

5 Similarly, the other zooplankton taxa were distributed high in the water column (10–20 m), whereas the fall of light intensity resulted in a migration upwards to the surface. It seems that appendicularia (*Oikopleura dioica*), meduses and doliolids responded to light changes and did move up in the water column towards the surface. Pteropods that maintained themselves mainly at 0–10 m increased their abundance before totality, while chaetognaths did not respond to light changes during the eclipse.

10 Avoidance of light by zooplankton has been demonstrated by many studies with a remarked preference for the surface layers during dawn and dusk (Conover et al., 1988; Hays et al., 1974). Earlier reports for *Pseudocalanus* and *Calanus* species (Runge and Ingram, 1991; Hattori and Saito, 1997), showed that medium to large calanoids exhibited a normal diel vertical migration moving upward into the surface layer sometime between 19:00 h and midnight. *Calanus* is a fast swimmer moving in short bursts of about 15–66 m/h (Marshall and Orr 1955). In a study of the diurnal vertical movements of chaetognaths and appendicularia, Schmidt (1973) reported that these animal groups during daytime avoid the upper layers, although around sunset and sunrise they tend to accumulate above 25 m. Consistent with our results are Sherman and Honey (1972) data, reporting that chaetognaths showed little change in vertical distribution during the eclipse. However the strong responses reported by Pepita (1955) for chaetognaths and decapod larvae differed from our results, probably due to species composition of the zooplankton.

## 25 4 Summary and conclusions

The solar eclipse of 29 March 2006 had very important effects on ecosystems, both on plants and marine zoo-plankton, which have been investigated in a parallel field

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experiment.

The diurnal course of photosynthetic rate for the seven important field-grown cereal and leguminous crops studied here, indicated a dramatic drop during the total phase of the eclipse. The minimum values of observed photosynthetic rates varied among the different species and ranged between 3.13 (faba beans) and 10.13  $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  (bread wheat). Cereals were less influenced than legumes and in particular faba beans, oats and grass pea were the most intensely affected. The latter may enable their use as potential indices for future investigation of the effects of climate changes on field crops.

The instantaneous changes observed in the diurnal cycle of stomatal conductance ( $g_s$ ) for the examined species could not be attributed to solar eclipse. Thus, since solar irradiance attenuation has not at the same time induced stomatal closure, thus not blocking  $\text{CO}_2$  uptake by plants, it is probably other endogenous factors that has been responsible for the observed fall in photosynthetic rates. This should be taken under serious consideration for planning of future solar eclipse related experiments.

The solar eclipse induced effects on the marine environment were mainly driven by the change of underwater irradiance. Model estimated photosynthetically active radiation (PAR) just below the water surface was  $\sim 2000 \mu\text{mol phot m}^{-2} \text{ s}^{-1}$  just before the 1st contact. Temperature and salinity remained almost constant during the eclipse event. Chl-a concentration varied from 0.14 to 0.19  $\mu\text{g l}^{-1}$ . No significant changes in chl-a vertical distribution were observed during the eclipse event.

The behavior of marine populations has been investigated, separately for micro-zooplankton (ciliates) and meso-zooplankton. Ciliates, tending to accumulate at 30 m depth, responded to the rapid decrease in light intensity during the eclipse and adopting night-time behaviour showed a vertical homogenous spreading in the water column. At this time, surface PAR had already decreased by  $\sim 50\%$ . From the mesozooplankton assemblage, *Calanus* and *Clausocalanus* copepodites having been synchronized with the exogenous changes, showed a vertical migratory movement towards the surface. Among the other copepodites, *Paracalanus*, *Oithona plumifera* as well as *Oncea*

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*media* increased their abundance in the surface layer before totality. The other copepodites, male and female copepods displayed no significant differences in distribution and apparent response to the eclipse. Similarly, the other zooplankton taxa such as appendicullaria (*Oikopleura dioica*), meduses and doliolids responded to light changes moving up towards the surface.

Overall, given the biodiversity of the Greek territory we seized the opportunity of the March 2006 Total Solar Eclipse to investigate the sensitivity of various species in the biosphere. The different responses ascertained between various species both in field crops and marine zoo-plankton, provide an early alert that future climate changes influencing the amount of radiation that reaches the earth's surface, may disturb the stability of the ecosystems, with direct and indirect impacts on crop productivity and in some cases on food chain it self.

*Acknowledgements.* We would like to thank the crew of the oceanographic R/V AEGAIO for their contribution.

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**Table 1.** Micro-zooplankton and meso-zooplankton samplings before, during and after the total solar eclipse at Kastelorizo marine station (max depth 290 m).

Cast	Time (UTC)	Zooplankton Micro-	Measurements Meso-
K1	7:52	+	+
K2	9:00		+
K3	9:40	+	+
K4	10:20	+	+
K5	11:20	+	+
K6	12:50	+	+
K7	14:15	+	

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**Table 2.** Maximum photosynthetic rates observed before the beginning of the eclipse and minimum photosynthetic rates near totality, for the examined species. The minimum/maximum ratios are also shown.

Species	Photosynthetic rates $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$		
	Max before	Min at totality	Min/Max
<i>Triticum durum</i>	26.70	7.08	0.2651
<i>Triticum aestivum</i>	22.47	10.13	0.4508
<i>Avena sativa</i>	27.59	5.41	0.1961
<i>Hordeum vulgare</i>	27.26	8.89	0.3261
<i>Lathyrus sativus</i>	21.66	4.61	0.2128
<i>Pisum sativum</i>	28.52	9.87	0.3461
<i>Vicia faba</i>	19.12	3.13	0.1637

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**Table 3.** Diurnal changes in stomatal conductance as least means ( $\text{mmol g H}_2\text{O m}^{-2} \text{s}^{-1}$ ), of four cereals and three leguminous species during the 29 March 2006 eclipse, at AUA experimental field. Values followed by the same letter are not statistically significant at the 95% significance level.

Time (UTC)	Crop field species													
	Hard wheat		Bread wheat		Oat		Barley		Lathurus		Pisum		Faba beans	
6:00	1.14	a	1.87	a	0.94	a	0.47	ab	2.1	a	1.58	a	0.9	a
7:00	0.66	b	0.8	bc	0.49	c	0.51	a	1.09	b	1.41	a	0.46	b
8:00	0.5	c	0.4	d	0.64	b	0.5	ab	0.52	cd	0.71	b	0.35	cd
9:00	0.31	de	1.08	b	0.35	d	0.33	c	0.42	cd	0.22	c	0.3	de
10:00	0.29	e	0.35	d	0.17	g	0.28	cd	0.27	d	0.41	bc	0.16	f
10:30	0.38	de	0.55	cd	0.25	efg	0.33	c	0.36	cd	0.38	c	0.34	cd
12:00	0.42	cd	0.41	d	0.29	def	0.43	b	0.62	c	0.3	c	0.22	ef
13:00	0.43	cd	0.3	d	0.2	fg	0.25	de	0.32	cd	0.2	c	0.35	cd
14:00	0.33	de	0.24	d	0.33	de	0.34	c	0.31	cd	0.25	c	0.24	ef
15:00	0.3	e	0.22	d	0.36	d	0.49	ab	–	–	–	–	0.4	bc
16:00	0.11	f	0.34	d	0.16	g	0.18	e	0.19	d	0.42	bc	0.21	ef

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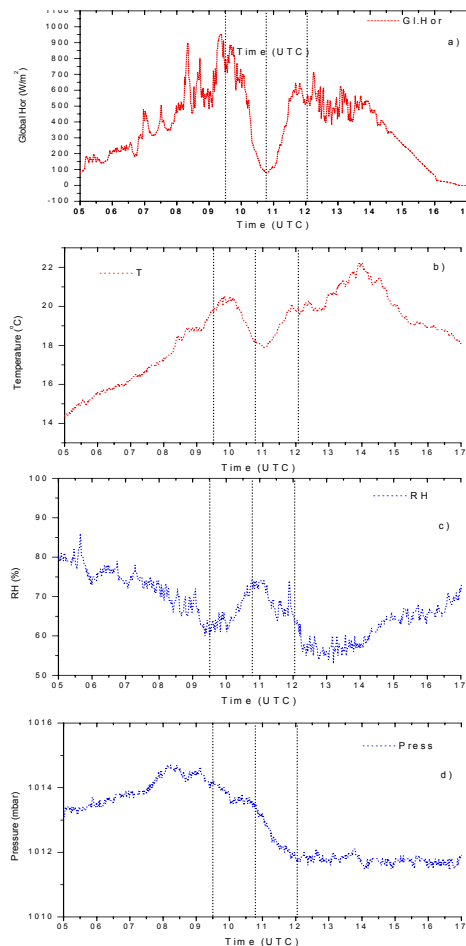
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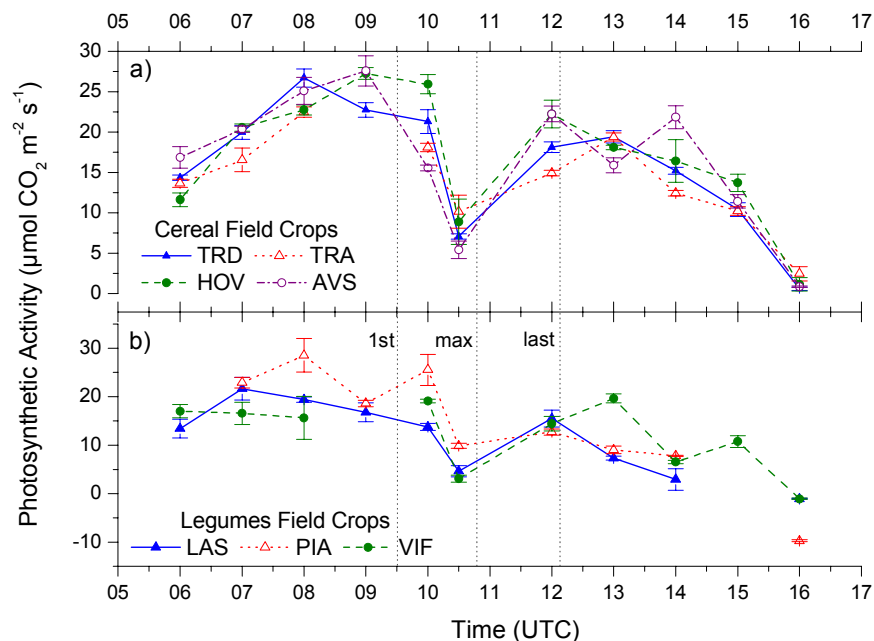


**Fig. 1.** The diurnal course of meteorological parameters **(a)** Global Horizontal Irradiance, **(b)** Temperature, **(c)** Relative Humidity and **(d)** Pressure, during 29 March 2006, at Thission station, Athens (National Observatory of Athens).

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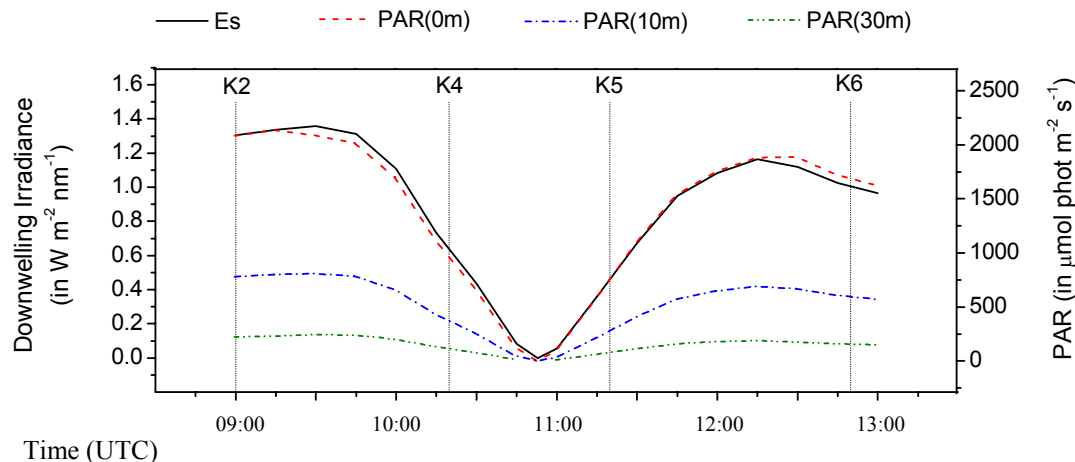


**Fig. 2.** Diurnal changes in CO<sub>2</sub> assimilation rate ( $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ ), of four cereals and three leguminous species during 29 March 2006 eclipse, at AUA experimental field (TRD- *Tr. durum*, TRA- *Tr. aestivum*, HOV- *H. vulgare*, AVS- *A. sativa*, LAS- *Lathurus sativus*, PIA- *P. arvense*, VIF- *V. faba*).

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**Fig. 3.** (Left axis) Change in measured downward surface irradiance (in  $\text{W m}^{-2} \text{nm}^{-1}$ ) at 550 nm during the eclipse event (solid line). (Right axis) Change in model estimated photosynthetically active radiation (PAR, in  $\mu\text{mol phot m}^{-2} \text{s}^{-1}$ ) just below the water surface ( $z=0$  m, dash line), at 10 m depth (dash-dot line), and at 30 m depth (dash dot dot line). The exact times of the casts K2, K4, K5 and K6 are shown as vertical dash lines.

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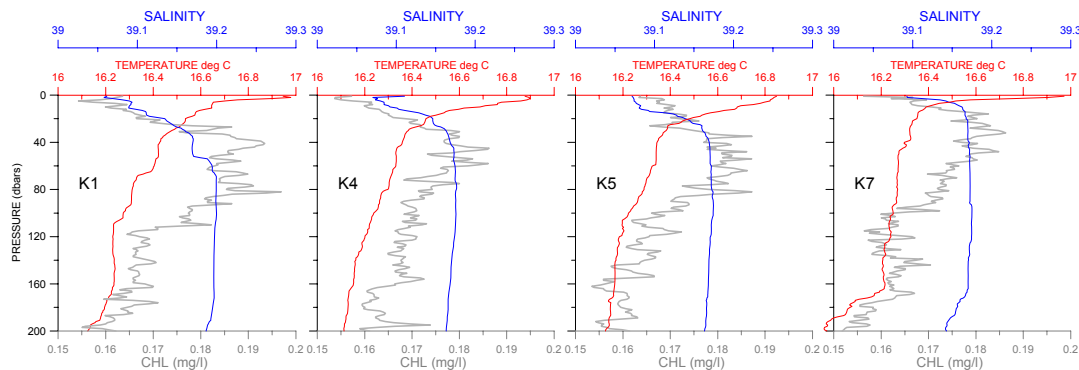
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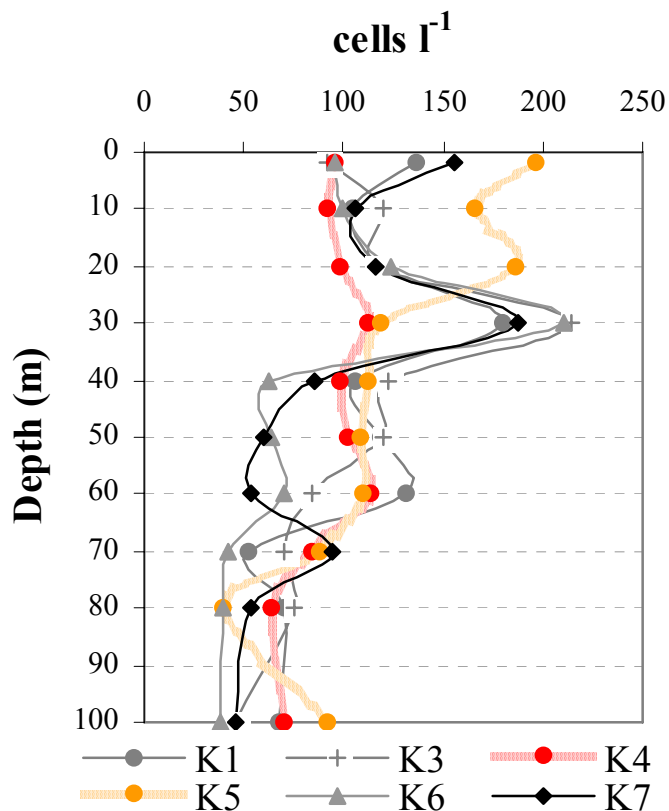


**Fig. 4.** Distribution of Temperature (red line), Salinity (blue line) and Chlorophyll-a (grey line) versus depth (down to 200 m). The profiles K1 and K7 represent the water column before the first contact and after the last contact, respectively. The profiles K4 and K5 are taken before and after the maximum of the eclipse.

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**Fig. 5.** Vertical distribution (abundance  $l^{-1}$ ) of ciliates during different sampling hours. K1 and K7 correspond to the first contact and the last contact, respectively. K4 and K5 are taken before and after the maximum of the eclipse.

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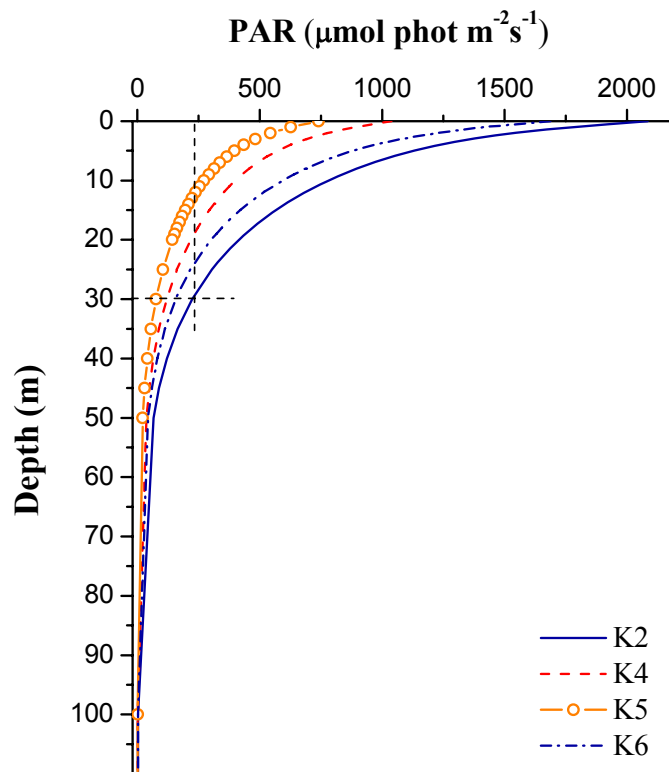
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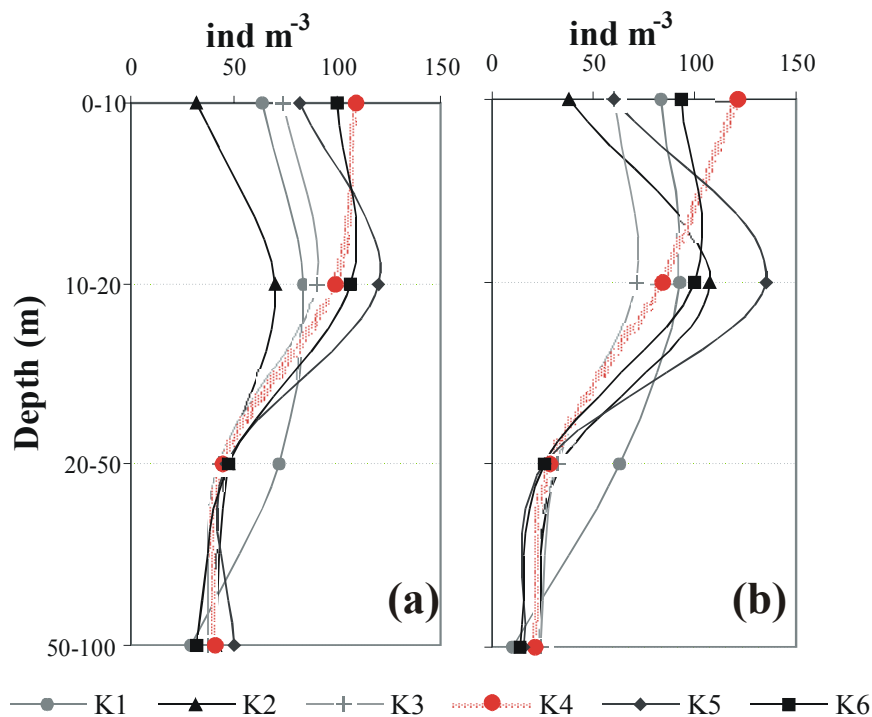


**Fig. 6.** Vertical profiles of PAR during different sampling hours. The exact time of casts K2, K4, K5 and K6 is shown in Fig. 3.

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**Fig. 7.** Vertical distribution (abundance  $m^{-3}$ ) of **(a)** copepods and **(b)** other mesozooplankton taxa during different sampling hours. K4 is taken before the maximum of the eclipse.

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